Taxonomic revision of some Recent agglutinated foraminifera from the Malay Archipelago, in the Millett Collection, The Natural History Museum, London

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SYNOPSIS. Eleven species of Recent agglutinated foraminifera in the Millett Collection from the Malay Archipelago, have been re-examined and revised systematically. They were originally described and illustrated in 1899 and 1900 with excellent lithographic drawings in the hand of Millett. With rare exceptions, the actual figured specimens, though not marked as such, have been recognised in his Collection. The species are here redescribed, re-illustrated by SEM photography and, where necessary, supplemented by new data, notably from similar environments in Brazil. All, with the exception of *Paratrochammina simplissima* (Cushman & McCulloch) and possibly *Trochammina? milletti* sp.nov., are brackish-water forms.

New taxa arc *Trunculocavus durrandi* gen. et sp.nov. and *Trochammina? milletti* sp.nov. A lectotype is designated for *Acupeina triperforata* (Millett), while *Ammobaculites salsus* var. *distinctus* Cushman & Brönnimann is clevated to specific rank and placed in *Ammotium*. All the species reviewed in this paper belong to the Suborder Trochamminina.

INTRODUCTION

Durrand (1898) gives what locality information there is about the Malay samples from which Fortescue William Millett made his classic study of the foraminifera. Durrand had for several years, out of his own interest, obtained small samples from around the SW Pacific and had examined them for the microscopical fauna and flora. In 1889 he had succeeded in getting the Netherlands India Steam Navigation Company (then controlled by the British India Steam Navigation Company) . . . 'to instruct the commanders of their fleet plying about the islands of the Archipelago, to collect bottom from each port of call'. The 'cleaned material' was picked over first by Durrand and then the foraminifera were determined by Millett and published (1898-1904) in 17 parts in the Journal of the Royal Microscopical Society. In all, 468 species and varieties were listed by Millett, 45 of them new. The descriptions were accompanied by 19 plates of guite exceptional and accurate drawings, from Millett's own hand.

The samples came from anchor mud where the ships were moored, more or less close inshore . . . 'in about 12 or 14 fathoms' (22–25 m). Unfortunately, a number of labels on the flasks of sediment became illegible through getting soaked by leakage, so the locality information is somewhat sketchy. The original samples each contained about 4 lbs (1.8 kg) of solid matter.

The material came from two areas. Area 1 ('from Celebes in the north and west, to Java in the south and New Guinea,

* Deceased 6.1.1993.

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Aru, and the Islands in the east, including such stations as Banda, Amboina, Flores, Sumbawa and Timor') contains stations 1–16; area 2 ('Singapore in the north, Banka in the south, Sumatra in the west, and Borneo in the east') contains stations 17–31.

As part of a major revision of shallow-water agglutinating foraminifera of the Indo-Pacific region (see also Brönnimann *et al.* 1992), eleven species belonging to the Trochamminina are here redescribed, and illustrated by scanning electron microscopy for the first time. The fauna has, for the most part, strong affinities with the foraminifera of brackish, mangrove sediments from other parts of the tropics, notably Brazil. Comparison is therefore made with material described by us (Brönnimann & Zaninetti, 1984*a*; *b*; Zaninetti *et al.*, 1977) from the mangroves of Guaratiba, Acupe and Baia de Sepetiba, Brazil.

For a recent review of mangrove foraminifera in general and their potential for palaeoenvironmental interpretation, the reader is referred to an important paper by Culver (1990).

LOCALITY INFORMATION

Of relevance to the present revision are the following stations from whence the specimens came; where the name of the station is not mentioned, the label has become illegible. The sample descriptions are in Durrand's own words.

Area 1 Station 2 [no locality]. Plastic mud, brownish tinted, rich in floatings.

Station 3 [no locality]. Brownish mud with lumps of blueish clay throughout, residue about one quarter-pound and floatings small.

Station 5 [no locality]. Blue ooze, residue and floatings small. Station 9 [no locality]. Results poor.

Station 11 [no locality].

Station 12 [no locality].

Station 12 [no locality]. Station 13 [Segaar, New Guinea, coral sand and mud, residue about six ounces, floatings rich]. Station 15 [no locality].

Area 2 Station 17. Muntok Banka, blue mud, residue eight ounces, floatings rich.
Station 19 [no locality]. Earthy coloured, river-looking mud, few foraminifera.
Station 21. Paney, northeast coast of Sumatra.
Station 27 [no locality].
Station 28 [no locality].

Durrand (1898:257) adds a postscript, stating that . . . 'it is important to bear in mind all this series was obtained from shallow water close inshore . . .'. It is clear from the agglutinating foraminifera revised here, that most of the localities were in fact brackish, associated with mangroves.

SYSTEMATIC DESCRIPTIONS

Order FORAMINIFERIDA Eichwald, 1830 Suborder TROCHAMMININA Brönnimann & Whittaker, 1988

Apart from the hierarchy listed above, no further suprageneric taxa will be used. Until we can be certain that the families and superfamilies of agglutinating foraminifera used by Loeblich & Tappan (1987) represent homogeneous units with respect to the wall structure, then it is better, for the present, not to use them. Similarly, genera are used in 'inverted commas' when the wall structure of their type species has not yet been examined. The eleven species described here, at least, all have a Trochamminina-type wall, defined by Brönnimann & Whittaker (1988) as . . . 'consisting of organic and agglutinated phases. Agglutinant bound by organic cement and outer and inner organic sheets. Devoid of perforations or alveolar pseudopores'.

The synonymies are not meant to be comprehensive, they are selective, merely listing the original reference, junior synonyms, changes of generic combination and important citations from the study area.

Genus ACUPEINA Brönnimann & Zaninetti, 1984b

TYPE SPECIES. Haplophragmium salsum Cushman & Brönnimann, 1948a (= junior subjective synonym of Haplophragmium agglutinans d'Orbigny var. triperforata Millett, 1899).

Acupeina triperforata (Millett, 1899) Figs 1.2, 13–15

- 1899 Haplophragmium agglutinans d'Orbigny var. triperforata Millett: 358(pars); pl. 5, figs 2a,b (lectotype) only; non figs 3a,b.
- 1948a Haplophragmium salsum Cushman & Brönnimann: 16,17; pl. 3, figs 10-13.
- 1965 *Lituola salsa* (Cushman & Brönnimann); Brönnimann & Zaninetti: 608–615; figs 1–3.
- 1984b Acupeina salsa (Cushman & Brönnimann); Brönnimann & Zaninetti: 219–222; figs A1–4, B1,2.
- 1984b Acupeina triperforata (Millett); Brönnimann & Zaninetti: 222 (addendum).
- 1988 Acupeina triperforata (Millett); Brönnimann & Whittaker: 112; pl. 4, figs 1–7.

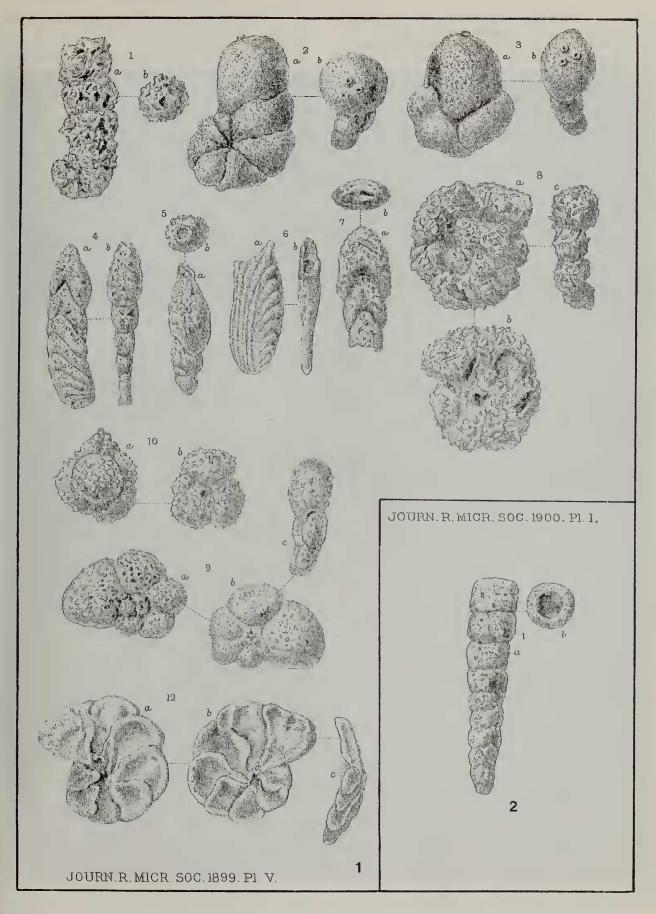
REMARKS. Millett (1899, pl. 5, figs 2,3; here reproduced as Figs 1.2, 3) illustrated four views of his new variety *triperforata*. Examination of the original material shows that two different brackish species are involved: *Acupeina triperforata* (Millett) and *Arenoparrella mexicana* (Kornfeld).

The individual drawn by Millett (1899, pl. 5, figs 2a,b; here reproduced in Fig. 1.2a,b) in side and apertural views, has been re-illustrated by SEM in Figs 13–15. The micrographs show side and edge views of a test, initially streptospiral then uniserial, and the detail of the multiple aperture which consists of three closely spaced, virtually equidistant pores (of around 25 μ m diameter) with upturned rims. Millett apparently believed that the aperture of his new variety invariably consisted of the three rounded pores, hence the name. The individual in Figs 13–15 is undoubtedly Millett's figured specimen and is here formally designated lectotype.

The specimen drawn by Millett (1899, pl. 5, figs 3a,b; reproduced here in Fig, 1.3a,b) in side and apertural views, has been re-illustrated by SEM in Figs 9-12 not only to show both sides of the test but the details of the composite aperture. Its morphology is quite different from the lectotype of H. agglutinans var. triperforata. It represents, in fact, a typical specimen of Arenoparrella mexicana (Kornfeld, 1931)(see below). It is unfortunate that Loeblich & Tappan (1987: 21, pl. 71, figs 3,4) illustrated this very specimen, together with the lectotype, as A. triperforata. It is also worth noting that Millett's pl. 5, fig. 3b is the edge view of fig. 3a, but as can be seen from our SEM illustration, rather misleading. It purports to show only three large pores with everted borders. In reality, it has a single oblique-perpendicular slit and 12 small peripheral pores of 5-6 µm diameter, devoid of rims. Closer examination of Millett's apertural view (see Fig. 1.3b) may just show the termination of the slit (the specimen is tilted forward), but the determination of the pores is still seriously in error.

Fig. 1.1–1.10, 1.12 Reproduction of part of Plate 5 of Millett (1899). The original identifications were as follows: Fig. 1.1, *Haplophragmium agglutinans* (d'Orbigny), ×112; Fig. 1.2, 3, *H. agglutinans* var. *triperforata* var.nov., ×112; Fig. 1.4–6, *H. cassis* (Parker), ×112; Fig. 1.7, *H. cassis* (Parker) or ?*Reophax*, ×75; Fig. 1.8, *H. compressum* Goës, ×75; Fig. 1.9, *H. nanum* Brady, ×112; Fig. 1.10, *H. anceps* Brady, ×56; Fig. 1.12, *Trochammina ochracea* (Williamson), ×75. Reproduced by permission of the Royal Microscopical Society.

Fig. 2.1 Reproduction of part of Plate 1 of Millett (1900). It was originally identified as *Bigenerina digitata* d'Orbigny var., ×169. Reproduced by permission of the Royal Microscopical Society.



Brönnimann & Zaninetti (1984b: 222, Addendum) have shown that *Haplophragmium agglutinans* d'Orbigny var. *triperforata* Millett (1899) is identical with *H.salsum* Cushman & Brönnimann (1948a), which is the type species of *Acupeina* Brönnimann & Zaninetti, 1984b.

LECTOTYPE. The individual illustrated by Millett (1899, pl. 5, figs 2a,b; Figs 1.2, 13–15 herein) is designated lectotype of *H. agglutinans* var. *triperforata*, now *Acupeina triperforata*. It is deposited in the collections of the BMNH, no. 1955.11.1.1076.

DIMENSIONS (LECTOTYPE). Height of test — $380 \ \mu\text{m}$; diameter of coiled portion — $235 \ \mu\text{m}$; maximum diameters of apertural pores — $25 \ \mu\text{m}$, with everted rims 4 μm high.

ENVIRONMENT. This species . . . 'is not uncommon at Station 9, and occurs also, but very sparingly, at Station 5' of Area 1. At Station 9, Millett (1899: 359) also reported *Haplophragmium cassis* (Parker) (= *Ammoastuta salsa* Cushman & Brönnimann and *Ammotium* spp.), all brackish water species. Both *Acuipeina triperforata* and *Arenoparella mexicana* are also exclusively brackish forms, occurring commonly in tropical to subtropical mangrove swamp sediments.

Genus AMMOSASTUTA Loeblich & Tappan, 1984

TYPE SPECIES. Ammoastuta salsa Cushman & Brönnimann, 1948a.

Ammoastuta salsa Cushman & Brönnimann, 1948a Figs 1.6, 35

- Haplophragmium cassis (Parker); Millett (pars): 359;
 pl. 5, figs 6a,b only (non figs 4,5,7) (non Lituola cassis Parker, 1870).
- 1948a Ammoastuta salsa Cushman & Brönnimann: 17; pl. 3, figs 14–16.
- 1970 Ammoastuta salsa Cushman (sic); Hofker: 3.
- 1986 Ammoastuta salsa Cushman & Brönnimann; Brönnimann: 29–44; figs 1–7. (q.v. for synonymy).

REMARKS. Millett (1899: 359, pl. 5, figs 6a,b; here reproduced as Fig. 1.6a,b) figured side and edge views of a slightly damaged, but clearly recognizable specimen of *Ammoastuta* salsa under the name of *Haplophragmium cassis* (Parker). He also illustrated two different species of *Ammotium* (pl. 5, figs 4a,b, 5a,b; Figs 1.4, 5) and, used for all these different morphologies the same name, as he thought . . . 'the Malay specimens of this species [*H. cassis*] are very variable in form, some of them being extremely compressed, and composed of numerous chambers'.

The SEM photograph of the side view (Fig. 35), although now slightly more damaged, is demonstrably of the same specimen as in Millett's drawing. The tight initial coil cannot be seen, but on the other hand, the final two chambers of the juvenile stage are clearly visible. The adult consists of at least 7 elongate uniserial chambers which make up the main portion of the compressed test.

Brönnimann's (1986) morphological revision of *A. salsa* has shown that the test starts with a tight early spiral consisting only of a proloculus and deuteroloculus. On the basis of this arrangement, *Ammosastuta* is correctly placed in the Lituolidae. Loeblich & Tappan (1987: 79) accepted this interpretation, but stated that the second chamber is growing in the . . . 'opposite direction' (without saying in respect to what). This is simply not the case. The second chamber develops from a porus in the side of the proloculus. It is just the normal forward continuation, considering the flow of the protoplasm, which produces the elongate deuteroloculus with a porus at its apex. Hence the embryonic chambers form a tight, reduced spiral (see Brönnimann, 1986: 32, fig. 3).

Ammoastuta salsa is occasionally placed in synonymy with Ammobaculites (=Ammoastuta) ineptus Cushman & McCulloch, 1939. Cushman & Brönnimann (1948a) regarded the two as distinct, as did Brönnimann (1986). An examination by Brönnimann of the two paratypes of A. ineptus, deposited in the collections of the U.S. National Museum of Natural History, Washington, confirms this separation. Of the paratypes, only one, registration no. 35826, is well preserved. It is definitely an Ammoastuta, but differs from the compressed A. salsa by having a strongly inflated test.

DIMENSIONS OF FIGURED SPECIMEN (BMNH no. 1955.11.1.1121). Maximum height (damaged) — 280 µm.

ENVIRONMENT. Recorded from Station 9, Area 1. It occurs together with *Acupeina triperforata*, *Ammotium* spp. and *Arenoparella mexicana*, all typical brackish water species.

Genus AMMOBACULITES Cushman, 1910

TYPE SPECIES. *Spirolina agglutinans* d'Orbigny, 1846. Lectotype designated by Loeblich & Tappan (1964: C241, figs 251.6a,b).

REMARKS. The genus *Ammobaculites* Cushman (1910) contains free agglutinated tests with a simple interior; the early portion is planispiral, the later part uncoiled and rectilinear. It is radially-symmetrical in transverse section. The single aperture is terminal, areal and radially symmetrical. The wall structure of the type species is unknown.

This definition is more restrictive than Loeblich & Tappan's (1987: 74) as it not only excludes streptospiral and trochospiral initial coils, but also laterally compressed tests. The transverse sections of the chambers of the uncoiled portion of the test and the outlines of the terminal apertures are radially symmetrical; these features are regarded as important generic criteria.

The wall structure of *Ammobaculites exiguus*, the species in the Millett Collection, is of the Trochamminina type. If A.

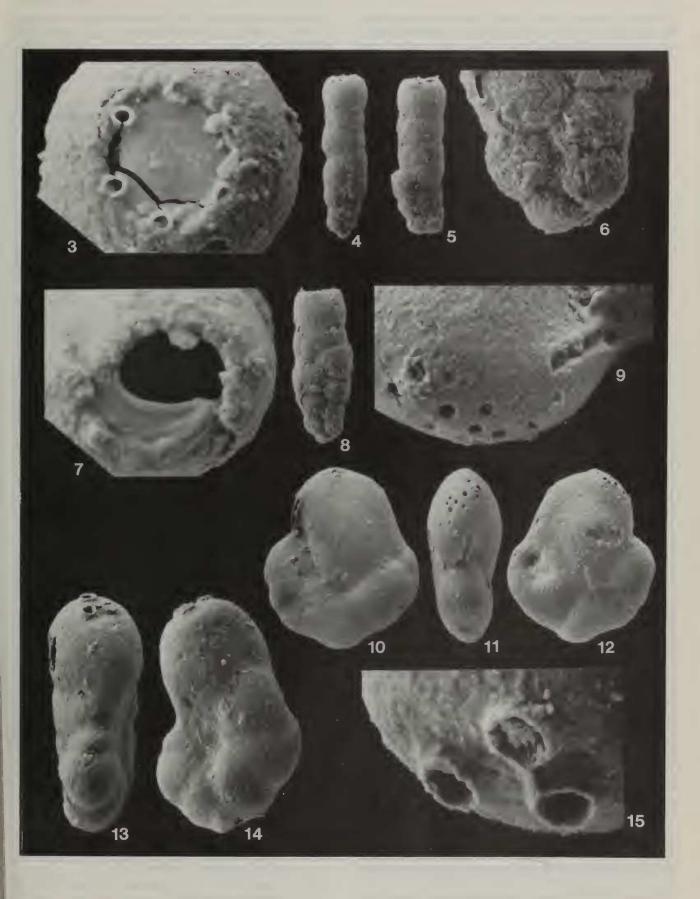
All from the Millett Collection, Malay Archipelago.

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Figs 3–8 *Trunculocavus durrandi* gen. et sp.nov. Figs 3,4, Detail of aperture (×900) and side view (×160), respectively. Holotype, BMNH no. 1955.11.1.187; Fig. 5, Side view (×175). Paratype, BMNH no. 1911.11.1.189; Figs 6–8, Detail of initial coil (×540), aperture (×730) and side view (×160), respectively. Paratype, BMNH no. 1955.11.1.188.

Figs 9–12 Arenoparrella mexicana (Kornfeld). Detail of apertures (×480), side, edge and view of other side (×160), respectively. BMNH no. 1955.11.1.1075.

Figs 13–15 Acupeina triperforata (Millett). Edge and side view (×160) and detail of aperture (×700), respectively. BMNH no. 1911.1..1076.



agglutinans, the type species, should have the same wall type, then *exiguus* would be correctly placed in *Ammobaculites*. If not, then it would have to be placed in a new genus. In view of these uncertainties, *Ammobaculites* is placed in inverted commas in our treatment of 'A'. *exiguus*.

"Ammobaculites" exiguus Cushman & Brönnimann, 1948b Figs 1.1, 42–44

- Haplophragmium agglutinans (d'Orbigny); Balkwill & Wright: 330; pl. 13, figs 18?, 19,20 (non d'Orbigny, 1846).
- 1899 Haplophragmium agglutinans (d'Orbigny); Millett: 357, pl. 5, figs 1a,b.
- 1938 Ammobaculites agglutinans (d'Orbigny); Bartenstein: 391; fig. 14.
- 1948b Ammobaculites exiguus Cushman & Brönnimann: 38; pl. 7, figs 7,8.
- 1952b Ammobaculites cf. exiguus Cushman & Brönnimann; Parker: 443;pl. 1, figs 16,17.
- 1952 Ammobaculites agglutinans (d'Orbigny); Rottgardt:
 180; pl. 1, fig. 4. 1954 Ammobaculites exiguus Cushman & Brönnimann; Phleger: 633; pl. 1, fig. 5.
- 1956 Ammobaculites sp. B, Warren: 139; pl. 1, figs 22-24.
- 1957 Ammobaculites exiguus Cushman & Brönnimann; Todd & Brönnimann: 23; pl. 2, fig. 7.
- Ammobaculites exiguus Cushman & Brönnimann; Benda & Puri: 335; pl. 1, fig. 15. 1973 Ammobaculites balkwilli Haynes: 25–27; pl. 2, figs 2,3; pl. 29, figs 5,6; text-fig. 4.1–5.
- 1978 Ammobaculites dilitatus (sic) Cushman & Brönnimann; Schafer & Cole: pl. 3, fig. 9 (non Cushman & Brönnimann, 1948b).
- 1980 Ammobaculites dilatatus Cushman & Brönnimann; Scott & Medioli: 35; pl. 1, figs 9,10.
- ?1983 Ammobaculites exiguus Cushman & Brönnimann; Haman: 72; pl. 5, figs 1–4.
- 1983 Ammobaculites diversus Cushman & Brönnimann; Haman: 72; pl. 4, figs 14,15 (non Cushman & Brönnimann, 1948b).
- 1986 Ammobaculites exiguus Cushman & Brönnimann; Brönnimann & Keij: pl. 3, fig. 7.

REMARKS. Millett (1899: pl. 5, figs 1a,b; here reproduced as Figs 1.1a,b) illustrated, without description, a typical specimen of *exiguus* under the name of *Haplophragmium agglutinans* (d'Orbigny). The same specimen (BMNH no. 1955.11.1.1057) is re-illustrated by SEM in our Figs 43,44. The oblique view (Fig. 43) shows the radially-symmetrical areal and terminal aperture, which is larger than in Millett's drawing. It is not bordered by a rim as that shown by Haman's (1983, pl. 5, figs 1–4) 'A. *exiguus*', which may represent a different species. Millett's specimen has four uniserial chambers which follow from a planispiral, tightly enrolled early test. The agglutinant is coarse and the sutures in the initial portion are not well defined; on the uniserial portion, they are distinct, however, and run perpendicularly to the elongate axis of the test.

Illustrated in Fig. 42 (BMNH no. 1911.11.1.1058) is a smaller, albeit damaged specimen, which is more typical of the size of the Malay material. Four radial sutures can be recognized in the coiled portion and there are three chambers in the uniserial part; the final chamber is crushed.

One of us (P.B.) has re-examined the holotype of A.

exiguus (registration no. 56761) in the U.S. National Museum of Natural History. Its overall morphology corresponds well with Millett's illustrated specimen of H. agglutinans. However, in its uniserial portion there are five chambers and the agglutinant is finer than in the Malay specimen. Nevertheless, the two both have a circular transverse section and a large radially-symmetrical, terminal aperture without a rim; the intercameral sutures run perpendicular to the elongate axis of the test, there being no suggestion of Ammotium-type sutures. In addition to the holotype of exiguus, there are two slides with paratypes: in slide no. 56762 there is a single paratype; under no. 56763 there are, amongst typical specimens, some very small individuals which differ from the type by their thin, elongate tests. These latter have also been encountered by us in the mangrove sediments of Acupe, Brazil. They represent a new species of brackish 'Ammobaculites' which will be published elsewhere. It should be noted that 'A'. exiguus and this new, minute species, are the only true representatives of 'Ammobaculites' occurring in brackish waters.

DIMENSIONS OF FIGURED SPECIMEN (BMNH no. 1911.11.1.1057). Height of test — 385 μ m; diameter of initial planispiral portion — 135 μ m; diameter of final chamber — 125 μ m; diameter of aperture — 50 μ m.

ENVIRONMENT. In the Millett Collection, specimens are labelled 'Haplophragmium agglutinans' from stations 2,9,12,14,15,19,21 and 27; Millett notes (p. 358) that . . . 'the specimens are all minute, and although they occur at most of the Stations, are not very numerous'. According to Parker *et al.* (1953), 'A'. *exiguus* is a species which lives in brackish as well as in marine waters.

Genus AMMOTIUM Loeblich & Tappan, 1953

TYPE SPECIES. Lituola cassis Parker (in Dawson), 1870.

REMARKS. Ammomarginulina Wiesner, 1931 (type species: A. ensis Wiesner, 1931) is a deep-water genus, with a morphology close to that of the supposedly exclusively brackish-water genus, Ammotium. After having compared the definitions of Ammomarginulina and of Ammotium in Loeblich & Tappan (1987), the question arises as to whether the two are really synonymous. The sutures of the former are, however, less slanting that those of Ammotium, and the test is strongly compressed. Of the shape of the aperture of Ammomarginulina ensis nothing is known except for the fact that it is rounded. Small morphological differences such as these may not be considered sufficient to retain the two genera. However, they seem to represent two disparate homogeneous environmental groups which, should this be sustained, must be separated taxonomically, even if the morphological differences were even less pronounced (see also Resig's (1982: 977-978, pl. 1, figs 3-5,9) description of Ammomarginulina hadalensis Resig from the Peru-Chile Trench, depth 5846 m). Clearly, the wall structure of Ammomarginulina must also be investigated.

Ammotium morenoi (Acosta, 1940) Figs 32–34, 54

- 1899 Haplophragmium cassis (Parker): 359 (pars) (non Lituola cassis Parker, 1870).
- 1940 Ammobaculites morenoi Acosta: 272; pl. 49, figs 3,8 (holotype) only (non Fig. 1).

- 1948a Ammobaculites salsus Cushman & Brönnimann: 16; pl. 3, figs 7a,b,8,9 (holotype figs 7a,b).
- 1952b Ammoscalaria fluvialis Parker: 444; pl. 1, fig. 24 (holotype) only (non fig. 25).
- 1953 Ammobaculites salsus (et vars.) Parker et al.: 5; pl. 1, figs 18–25 only (non fig. 17).
- 1954 Ammobaculites exilis Cushman & Brönnimann; Phleger: pl. 1, fig.6 (non Cushman & Brönnimann, 1948b).
- 1954 Ammobaculites salsus Cushman & Brönnimann; Phleger: pl. 1, fig. 7 only (non fig. 8).
- 1954 Ammoscalaria fluvialis Parker; Phleger: pl. 1, fig. 11.
- 1957 Ammobaculites salsus Cushman & Brönnimann; Todd & Brönnimann; 24, pl. 3, fig. 8
- 1958 Ammobaculites salsus Cushman & Brönnimann; Arnal: 37; pl. 98, figs 4-7.
- 1968 Ammotium salsum (Cushman & Brönnimann); Lutze: 25; pl.1, figs 5,6.
- 1978 Annmotium salsum (Cushman & Brönnimann); Poag: 405; pl. 5, figs 1–39.
- 1980 Annmotium salsum (Cushman & Brönnimann); Scott & Medioli: pl. 1, figs 11–13.
- 1983 Ammotium morenoi (Acosta); Haman: 72; pl. 5, figs 6–9.

REMARKS. The specimen illustrated by us in Figs 32–34 was not figured or described by Millett but comes from a slide in the Millett Collection labelled *Haplophragmium cassis* Parker (BMNH no. 1955.11.1.1118–1133) and was undoubtedly part of his concept of that species. It is a typical representative of *Ammotium morenoi*. The small test is axially compressed and consists of a short, completely coiled planispiral initial stage, followed by an uncoiled portion of about 5 low, elongate, laterally compressed chambers which on the interior side reach back toward the initial planispire. The single aperture is a narrow elongate slit with rounded extremities, situated at the apex of the final chamber, in a marginal or outer position.

Under the name of *H. cassis*, Millett (1899, pl. 5, figs 4a,b, 5a,b) did illustrate two specimens, which belong to different species of *Ammotium*. The latter (reproduced here as Fig. 1.5a,b) is the upper part of an *Ammotium pseudocassis* (Cushman & Brönnimann, 1948b)(see p., below) but was not found in the Millett Collection. The former (Fig. 1.4a,b) is a complete specimen of *A. directum* (Cushman & Brönnimann, 1948b) and is refigured in Fig. 31.

In addition to this specimen, we have also illustrated in Fig. 54, for the purpose of comparison, the lateral view of a typical specimen of *A. morenoi* from the mangrove sediments of Guaratiba, Brazil (see Zaninetti *et al.*, 1977). It consists of an initial, almost involute planispire, followed by two uniserial, laterally flattened, low and elongate chambers, which on the inner side extend backwards toward the early spire.

In common with other brackish foraminifera, *A. morenoi* is highly variable in its overall morphology, in particular in size and in outline of the test in lateral view. From small, almost triangular forms, as represented by the holotype of *morenoi* or the holotype of *Ammoscalaria fluvialis* Parker (1952b), we find all possible transitions to the elongate slender specimens of *Ammobaculites salsus* described by Cushman & Brönnimann (1948a) from Trinidad, or to the large and elongate individuals recorded by Poag (1978) from Gulf Coast estuaries. Brodniewicz (1965: 187–194, text–figs 21–25) has shown that a similar form, identified by her as *Ammotium cassis* (Parker), from the Baltic, is also characterized by a great morphological variability. She tried to distinguish six different morphological types on the basis of outline, chamber form, and dimensions of the test and chambers. A study of Brodniewicz's paper, however, suggests to us that it is virtually impossible to separate her different morphotypes.

DIMENSIONS OF FIGURED SPECIMENS (MALAY SPECIMEN, BMNH no. 1991.11.1.1122). Height of test — 170 μ m; width (length) — 105 μ m; thickness — 35 μ m.

(BRAZILIAN SPECIMEN). Height of test — 370 μ m; maximum width — 190 μ m; final chamber — 225 μ m high; maximum diameter of oblong aperture — 50 μ m.

ENVIRONMENT. Found only in Station 9 (Area 1) in association with Ammotium pseudocassis, A. directum, Acupeina triperforata, Ammoastuta salsa and Arenoparella mexicana, all typical brackish water species. A. morenoi is normally abundant in tropical and subtropical mangrove sediments but has also been recorded, albeit rarely, in brackish sediments of temperate climes (Parker, 1952b; Lutze, 1968). We have never encountered this species in the British Isles or in the Mediterranean.

OBSERVATIONS ON CERTAIN SYNONYMS AND NON-SYNONYMS (NEAR ISOMORPHS) OF *AMMOTIUM MORENOI* ACOSTA.

 Ammobaculites salsus Cushman & Brönnimann, 1948a and A. distinctus Cushman & Brönnimann, 1948b.

Haman (1983) was the first author to place Ammobaculites (=Ammotium) salsus into synonymy with Acosta's species. In the introduction to his paper, Acosta (1940: 269) wrote that the agglutinating species were rare in the shallow water assemblages from the Gulf of Santa Maria, Camaguey Province, Cuba, which were dominated by miliolids and nonionids. The Gulf of Santa Maria is bordered by extensive mangrove swamps. It is therefore assumed that the tests of the brackish agglutinated species, such as A.morenoi, had been transported by wave action into the marine environment of the open Gulf and were not in situ at the locality where Acosta collected them. Acosta (1940: 275) claimed to have deposited the types of his species in the Cushman Collection, which were later transferred from Sharon, Massachusetts to the U.S. National Museum of Natural History, Washington, D.C. A search by P.B. for the type specimen of A. morenoi proved unsuccessful and it seems that Acosta never did deposit his types in the Cushman Collection. Acosta's drawings (op.cit. pl. 49, figs 3,8, non fig. 1) leave no doubt, however, that Ammotium morenoi and A. salsum, originally described from Trinidad mangrove swamps, are one and the same.

When comparing the two 'species', the apertural view of the holotype of *Ammotium morenoi* (Acosta, 1940: pl. 49, fig. 8) is of interest. It shows a slit-like opening at the apex of the final chamber, in a marginal or outer position; the same type of aperture occurs in *A. salsum*. In both holotypes the peripheral outline of the initial planispire, as seen laterally, is perfectly rounded and not angular as in *Ammotium distinctum* (Cushman & Brönnimann (1948b: 40, pl. 7, fig. 14), which has also been described from the brackish mangrove sediments of Trinidad. This latter form was originally introduced as a variety of *Ammobaculites salsus*. As there are no intermediates between *distinctum* and *salsum*, the former is here elevated to specific rank. Authors, however, normally make no distinction between the two (see Phleger, 1954: pl. 1, fig. 8).

We have illustrated in Fig. 55 a lateral view in oil of *Ammotium distinctum*, from the mangrove sediments of Acupe, Brazil. The angular outline of the early planispire is clearly shown. The test begins with a relatively large proloculus of 65 μ m diameter, followed by a larger deuteroloculus of 75 μ m diameter. The total number of chambers in this specimen is eight, including the embryonic chambers. The height of the test is 220 μ m, width (length) 125 μ m, and length of aperture 45 μ m. Apart from the distinct angular periphery, there are no other important differences between *Ammotium morenoi* and *A. distinctum*.

2. Ammoscalaria fluvialis Parker, 1952b.

Parker (1952b: 444, pl. 1, fig. 24) first described this species from the Housatonic River, Long Island Sound, depth 3 m. From its association with other brackish species in her Facies 1, such as *Trochammina inflata, Jadammina macrescens* and *Miliammina fusca*, it can be inferred that *A. fluvialis* is also a brackish-water form. The morphology of the holotype is virtually identical with the holotype of *A. morenoi*, and for this reason we regard it as a junior synonym of the latter.

3. Lituola cassis Parker, in Dawson, 1870.

We have compared Ammotium morenoi with Lituola cassis Parker, the type species of Ammotium Loeblich & Tappan (1953). The lectotype of Ammotium cassis (BMNH no. ZF 4637), designated by Hodgkinson (1992), on our advice, is re-illustrated in Figs 38–41. It is from Gaspé Bay, Gulf of St. Lawrence, Canada, and came from the W.K. Parker Collection; it was collected in 16 fathoms (30 m), which suggests a marine environment, but the specimens could have been washed in from a brackish locality. Loeblich & Tappan (1987, pl. 60, figs 1,2) illustrate a 'Holocene' specimen from off Alaska in 223 m of water; should this specimen have been *in situ* it would further undermine the supposedly exclusively brackish nature of the genus, a factor that needs further investigation.

The lectotype clearly shows the initial planispire, then the uniserial inward slanting narrow and low chambers; the oblong aperture is at the apex of the final chamber, in a marginal or outer position (see also Goës, 1894, pl. 5, figs 152–157). The lectotype and paralectotypes are five times larger and much more massive than *A. morenoi*, though the two in several other respects are quite similar. It is our opinion that *A. cassis* should only be used for large and massive individuals, but at the same time we have our reservations that ecological factors (?marine salinities) may be responsible for the massive development of the *cassis* test (see also remarks above, on *A. cassis sensu* Brodniewicz (1965) from the Baltic). It is even three times the size of Poag's (1978) material from the Gulf Coast estuaries, the largest known specimens of *A. morenoi* from the tropics,

moreover Poag's specimens are very elongate and compressed with the uniserial portion quite unlike that of the true *cassis*.

The dimensions of the lectotype are: maximum height — 1600 μ m; maximum width — 785 μ m; maximum thickness — 360 μ m; thickness of planispiral portion — 125 μ m.

4. Ammobaculites prostomum Hofker, 1932.

This species was described by Hofker (1932: 87-91, text-figs 14a-f, 15a-d) from the Ammontatura, a part of the Gulf of Naples, with a depth of 150-200 m. The shapes of the illustrated specimens, seen laterally, particularly the short individuals (text-figs 14a and f), much resemble the small specimens of Ammotium morenoi such as our Fig. 54. On Hofker's short specimens the sutures are not shown fully, but on the larger specimens (text-fig. 15e) they are, toward the outer margin, at first outward slanting (not inward), then parallel up to the end of the uniserial portion. In lateral outline, these short specimens are near isomorphs of A. morenoi. However, the aperture is not placed asymmetrically, at the outer margin of the test as in Ammotium, but symmetrically in respect to the shape of the final chamber. For these reasons, Hofker's species does not belong to Ammotium. It is also a marine species and much resembles the group pf forms described and illustrated by Höglund (1947, pl. 31, figs 1a-g) from Björkholmen, Gullmar Fjord, from a depth of 30 m, under the name of Ammoscalaria pseudospiralis (Williamson).

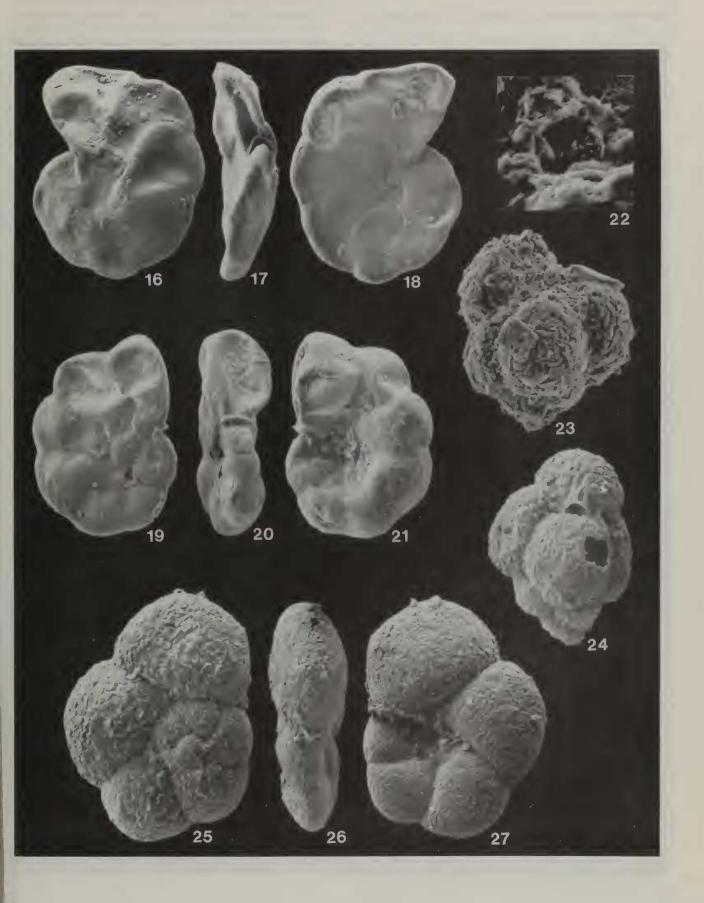
5. Ammoscalaria pseudospiralis sensu Höglund, 1947.

The genus Ammoscalaria was erected by Höglund (1947: 151-153) with Haplophragmium tenuimargo Brady (1884) as type species. Into his new genus he also placed Proteonina pseudospiralis Williamson, 1858. However, Ammoscalaria pseudospiralis was described by Höglund (1947: 159-162, pl. 31, figs 1a-p) exclusively from material obtained in the Gullmar Fjord, where it occurs commonly, and from the Skagerak, not on the basis of Williamson's material which was not available to him. The chambers of the rectilinear portion of this marine species are 'irregularly rectangular in lateral view' and there are 'no external sutures'. The oblong aperture is in a symmetrical position in respect to the final chamber and not asymmetric, as in Ammotium. We therefore do not regard Höglund's species as a synonym of pseudospiralis, although certain smaller specimens could be regarded as isomorphs of Williamson's taxon, particularly when seen in lateral view (e.g. pl. 31, figs 1m,n). Rather, Höglund's form is most probably a junior synonym of Ammobaculites (=Ammoscalaria) prostomum Hofker, 1932.

Figs 16–21 'Haplophragmoides' wilberti Anderson. Figs 16–18, Side, edge and view of other side (×115). BMNH no. 1911.11.1.5003; Figs 19–21, Side, edge and view of other side (×160), respectively. BMNH no. ZF 5002. Specimen from Brönnimann sample BR146, Acupe, Brazil, for comparison.

Figs 22-24 Trochammina? milletti sp.nov. Figs 22,23, Detail of aperture (×1,700) and side view (×320), respectively. Holotype, BMNH no. 1911.11.1.1088; Fig. 24, Side view (×260). Paratype, BMNH no. 1955.11.1.1089.

Figs 25–27 Paratrochammina simplissima (Cushman & McCulloch). Spiral, edge and umbilical views (×170). BMNH no. 1955.11.1.1141. All from the Millett Collection, Malay Archipelago, except where stated.



Ammotium pseudocassis (Cushman & Brönnimann,

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1948) Figs 1.5, 50, 53

Haplophragmium cassis (Parker); Millett: 359 (pars);
 pl. 5, figs 5a,b only (non Lituola cassis Parker, 1870).

 1983 Ammoscalaria pseudospiralis (Williamson); Haman:
 72; pl. 5, fig. 5 (non Proteonina pseudospiralis Williamson, 1858).

REMARKS. This species was illustrated by Millett (1899, pl. 5, figs 5a,b; here reproduced as Fig. 1.5a,b) under the name of *Haplophragmium cassis* (Parker). It is an upper fragment of an elongate test consisting of three rounded (in transverse section), hardly compressed chambers. Millett's drawing shows the inward and backward trending sutures and the rounded aperture in marginal position. Within the concept of this species, Millett also included specimens of *Ammotium directum* (Cushman & Brönnimann)(Figs 1.4a,b, 31,?36) and *Ammoastuta salsa* Cushman & Brönnimann (Figs 1.6a,b, 35). As already mentioned, the fragment of *A. pseudocassis* illustrated by Millett in his pl. 5, figs 5a,b (see our Figs 1.5a,b) could not be found in his Malay collection.

For comparison, we have illustrated typical specimens in lateral view of *A. pseudocassis* from the mangrove sediments of Guaratiba, Brazil (see Zaninetti *et al.*, 1977), one by SEM (Fig. 50), the other by optical photography in immersion (Fig. 53). In the latter specimen the early spiral is reduced to two chambers, a relatively large proloculus of 50 μ m diameter, and a larger deuteroloculus of about 75 μ m diameter. The embryonic chambers are not enclosed by other spiral chambers, as in *A. pseudospirale* (Williamson, 1858). The total number of chambers, including embryonics, is eight.

Ammotium pseudocassis differs from A. pseudospirale by the elongate, somewhat incurved test, the less compressed and elongate chambers and the reduced initial spire. The final chamber is usually the dominant one, making up about one-third of the test. It narrows toward the oblong aperture and extends on the inner side of the test toward the initial spiral. The early coil, represented by a reduced spire, consists of very few chambers only. A typical embryo consists of two very thin-walled chambers, a large proloculus, about 40-60 µm in diameter, and an equally large deuteroloculus. The embryo may form all the initial portion of the test. We have never found a microspheric specimen of A. pseudocassis and where the taxon is frequent, A. pseudospirale is usually absent. The aperture of the holotype of A. pseudocassis, deposited in the U.S. National Museum of Natural History (registration no. 56764), is not as circular as that shown in Millett's drawing, but distinctly oblong. As in Ammotium cassis and A. morenoi, the aperture is situated at the apex of the last chamber in a marginal position (see Cushman &

Brönnimann, 1948*b*, pl. 7, fig. 12b). However, it seems that, when the final chamber is hardly compressed, the aperture may become rather centred and more rounded than slit-like, but never completely circular.

DIMENSIONS. Fig. 50: Height of test — 480 μ m; maximum width — 150 μ m; height of final chamber — 290 μ m; maximum diameter of aperture — 50 μ m.

Fig. 52: Height of test — 575 μ m; maximum width — 170 μ m; height of final chamber — 375 μ m; maximum diameter of aperture — 75 μ m; thickness of wall (final chamber) 10 μ m.

ENVIRONMENT. The group of forms referred by Millett to H. *cassis* (Parker) occur only at Station 9, Area 1, . . . 'where they are not uncommon'. They are all exclusively brackish water species.

Ammotium directum (Cushman & Brönnimann, 1948b) Figs 1.4,(?1.7),31,36,37,45–47

- 1899 Haplophragmium cassis (Parker): 359 (pars); pl. 5, figs 4,?7 only (non Lituola cassis Parker, 1870).
- 1948b Ammobaculites directus Cushman & Brönnimann: 38; pl. 7, figs 3,4.
- 1956 Ammotium sp. D. Warren: 139; pl. 1, figs 19-21.
- 1957 Ammobaculites directus Cushman & Brönnimann; Todd & Brönnimann: 23; pl. 2, fig. 6 only (non Fig. 7).
- 1988 Ammotium casamancensis (sic) Debenay: 46,47; pl. 1, figs 1–3.

REMARKS. Under the name of H. cassis (Parker), Millett (1899, pl. 5, figs 4a,b; here reproduced as Figs 1.4a,b) illustrated a specimen of Ammotium directum (Cushman & Brönnimann). Our identification is based on the overall outline, the shape of the sutures, and the strong lateral compression of the test. The specimen illustrated by SEM in Fig. 31 is that very same specimen, viewed from the other side.

The fragment shown in Millett's fig. 7, which he compared to . . . 'a species of *Reophax*, with the plan of growth and chevron-shaped chambers of *Frondicularia*' may be that illustrated by SEM in Figs 36,45,46, although the chevron-shaped chambers are exaggerated, as they are in the drawing of fig. 4a (compare with our Fig. 31). The aperture in both specimens is slit-like, without an everted border, and is situated at the apex of the final chamber. For comparative purposes, a lateral view of a specimen of *A. directum*, from the mangrove sediments of Acupe, Brazil (BMNH no. ZF 4999) is illustrated in Fig. 47; the asymmetrical sutures are well exhibited.

The tests of Ammotium directum in the Millett Collection are extremely fragile, in contrast to those found in Trinidad

¹⁹⁴⁸b Ammobaculites pseudocassis Cushman & Brönnimann: 39, 40; pl. 7, figs 12a,b.

Figs 28-30 Trematophragmoides bruneiensis Brönnimann & Keij. Side, edge and view of other side (×115). BMNH no. 1955.11.1.1136.

Figs 31, 36, 37 Ammotium directum (Cushman & Brönnimann). Side views of three separate specimens (×185, 205 and 185, respectively). BMNH nos. 1955.11.1.1118–1120.

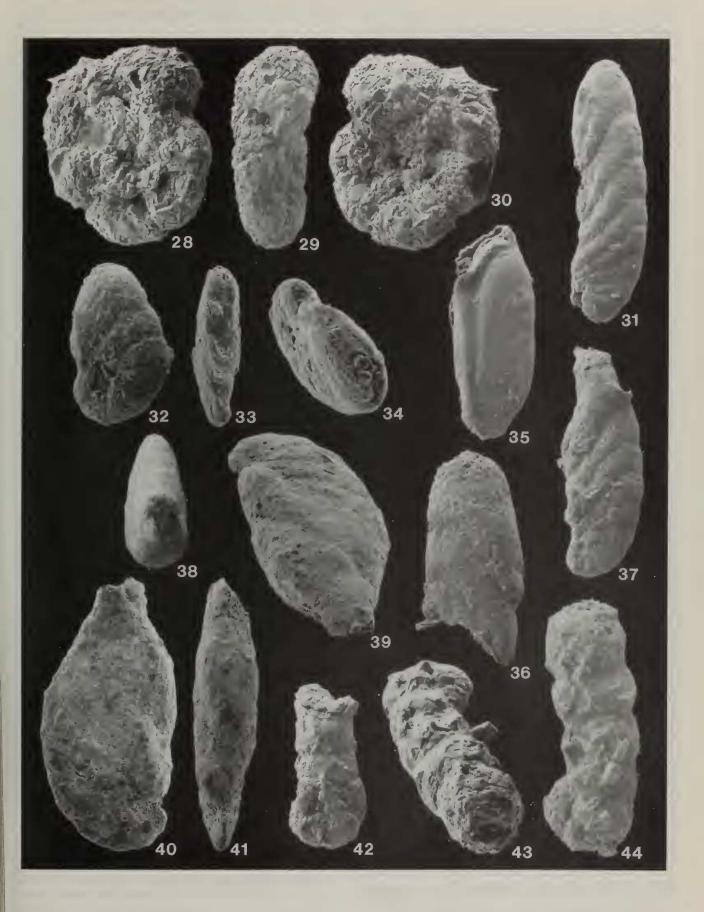
Figs 32-34 Ammotium morenoi (Acosta). Side, edge and oblique apertural views (×250). BMNH no. 1955.11.1.1122.

Fig. 35 Ammoastuta salsa Cushman & Brönnimann. Side view (×200). BMNH no. 1955.11.1.1121.

Figs 38-41 Ammotium cassis (Parker). Apertural, oblique apertural, side and edge views (×45). Lectotype, BMNH no. ZF 4637, Gaspé Bay, Gulf of St. Lawrence, Canada.

Figs 42-44 'Ammobaculites' exiguus Cushman & Brönnimann. Fig. 42, Side view (×185). BMNH no. 1955.11.1.1058; Figs 43,44, Oblique-apertural and edge views (×175). BMNH no. 1955.11.1.1057.

All from Millett Collection, Malay Archipelago, except where stated.



or Brazil. Cushman & Brönnimann (1948b) distinguished two species of *Ammotium* with strong lateral compression, namely *A. directum* and *A. diversum*. To these has to be added a third, *A. subdirectum* Warren, 1956.

Ammotium directum, the more common species, as described above, has strongly incurved sutures of an asymmetrical type with a shorter outer or marginal branch and a longer, inner branch, which slants toward the initial spire (see Fig. 47). Occasionally, some sort of chevron pattern is formed but rarely to the extremes indicated by Millett's drawing (pl. 5, fig. 4a; our Fig. 1.4a). A. directum is always characterized by this asymmetrical type of suture. The test, moreover, is strongly compressed laterally and the width of the flattened chambers does not increase much in the course of growth. The aperture is slit-like and situated at the apex of the final chamber, more or less in a marginal position. The initial spiral consists of several chambers.

A. diversum is less common than A. directum. The only significant difference lies in the sutural shape, which in the former in the final ontogenetic stage, is always more or less horizontal, slightly incurved and in extremes, no longer asymmetrical (see Cushman & Brönnimann, 1948b, pl. 7, figs 5,6). Furthermore, in this species, the sutures of the early uniserial portion are slanting inward toward the initial coil. Occasionally, there is a suggestion that the two are linked by transitional forms. Should the two be ultimately considered synonymous then we would prefer to retain A. directum, as this, although printed on the same page, was described first. For the time being, however, both are retained.

A. subdirectum was described by Warren (1957, pl. 4, figs 6-8) from the marshes of the Buras-Scofield bayou region of southeastern Louisiana. We have encountered it but rarely in the mangrove sediments of Acupe, Brazil and Warren himself (1957: 33) mentioned that . . . 'specimens were rare wherever found except in one of the polyhaline marsh samples'. Two specimens from Acupe (BMNH nos ZF 5000 and 5001) are illustrated in Figs 48,49,51,52 for comparison with the Malay species of Ammotium. A. subdirectum is a many-chambered species characterized by the same asymmetrical type of sutures as found in A. directum. In the final growth stages the sutures may become more or less symmetrical and arranged in a chevron-like pattern, as shown in Millett's drawing of the fragment illustrated in pl. 5, figs 7a,b; Fig. 1.7a,b. Figs 36,45,46 could represent this specimen which is part of either an A. subdirectum, or an A. directum as discussed above. Normally, A. subdirectum is about twice as long as A. directum and composed of more chambers. The test is slightly incurved and the width of the chambers, seen laterally, increases quite strongly towards the final chamber. The aperture is a narrow oblong slit, as in A. directum and A. diversum, and situated at the apex of the final chamber, more of less in a marginal position (see Figs 48,49,51,52). In all three species, the agglutinant is fine-grained and the surface of the test usually appears smooth, occasionally even somewhat glossy.

DIMENSIONS OF FIGURED SPECIMENS (BMNH no. 1955.11.1.1118). Height of test — 290 μ m; maximum width of final chamber — 73 μ m.

(BMNH no. 1955.11.1.1119). Height of fragment – 270 μm; length of apertural slit – 45 μm.

(BMNH no. 1955.11.1.1120). Height of test — 330 µm.

ENVIRONMENT. This species was found only at Station 9

(Area 1). It is a typical brackish-water species.

Genus ARENOPARRELLA Andersen, 1951a

TYPE SPECIES. *Trochammina inflata* (Montagu) var. *mexi-cana* Kornfeld, 1931.

Arenoparrella mexicana (Kornfeld, 1931)

Figs 1.3, 9–12

- 1899 Haplophragmium agglutinans d'Orbigny var. triperforata Millett: 358 (pars); pl. 5, figs 3a,b only; non figs 2a,b.
- 1931 *Trochammina inflata* (Montagu) var. *mexicana* Kornfeld: 86; pl. 13, figs 5a–c.
- 1951a Arenoparrella mexicana (Kornfeld); Andersen: 31; fig. 1a-c.
- 1951b Arenoparrella mexicana (Kornfeld); Andersen; 96; pl. 11, figs 4a-c.
- 1977 Arenoparrella mexicana (Kornfeld); Zaninetti et al.; pl. 2, figs 3,7.

REMARKS. One of Millett's illustrated specimens (1899, pl. 5, figs 3a,b; reproduced here as Figs 1.3a,b) of H. agglutinans var. triperforata is, in fact, a typical specimen of Arenoparrella mexicana (Kornfeld). It is refigured here by SEM (Figs 9-12) and shows that the original drawing of the edge view in particular, is very misleading. As discussed above under the description of the lectotype of Acupeina triperforata (Millett), the edge view of fig. 3b also suggests that there are only three large everted apertures. The reality is an aperture consisting of a vertical slit lined by slightly uplifted borders, in an interiomarginal position, of about 50 µm length and 8 µm width, and 12 small, irregularly arranged, rounded pores above this primary aperture, of between 5 and 10 µm diameter, devoid of everted rims. Millett's specimen (BMNH no. 1955.1.1.1075) is tilted so far forward in apertural view that the primary vertical slit, so clearly visible in fig. 3a, might not have been seen, but it is puzzling to understand why he illustrated the apertural pores as he did. Millett's material from stations 5 and 9 quite clearly represents both Acupeina triperforata and Arenoparrella mexicana, which is not surprising as they commonly occur together. The illustrated specimen of the latter is completely involute (hence the small axial depression is closed). The final whorl consists of 4, axially compressed chambers which gradually increase in size with growth. In edge view the periphery is rounded. Umbilical and spiral sutures are poorly defined and the agglutination is rather fine-grained and produces a smooth surface.

DIMENSIONS OF FIGURED SPECIMEN (BMNH no. 1955.11.1.1075). Maximum diameter — 290 µm; minimum diameter — 240 µm; axial height (thickness) — 120 µm.

ENVIRONMENT. See under *Acupeina triperforata* (p.). *Arenoparella mexicana* is a typical tropical and subtropical mangrove swamp species.

Genus HAPLOPHRAGMOIDES Cushman, 1910

TYPE SPECIES. Nonionina canariensis d'Orbigny, 1839.

REMARKS. The wall structure of the type species is unknown; we are not even sure of the apertural position, for that matter. Although the wall of *H. wilberti*, the species in the Millett Collection, is of the Trochamminina-type (see below), we prefer, in our treatment of this species, to use *Haplophragmoides* in inverted commas, until more is known about *canariensis*.

'Haplophragmoides' wilberti Andersen, 1953 Figs 1.12, 16–21

- 1899 Trochannina ochracea Williamson; Millett: 363, pl. 5, figs 12a-c (non Williamson, 1858).
- 1953 Haplophragmoides wilberti Andersen: 21, pl. 4, figs 7a,b.
- 1961 Haplophragmoides wilberti Andersen; Todd & Low: 133; pl. 1, fig. 5.
- 1973 Haplophragmoides wilberti Andersen; Haynes: 27–30, pl. 2, fig. 1; pl. 29, fig. 7?; text-figs 5.3–7.
- 1977 Haplophragmoides wilberti Andersen; Zaninetti et al.: pl. 1, figs 12,13.
- 1981 *Trochammina* sp., Cann & de Deckker: 668, pl. 2, figs 1–19.
- 1983 Haplophragmoides wilberti Andersen; Haman: 71; pl. 3, figs 14,15.

REMARKS. On re-examination, Millett's (1899, pl. 5, figs 12a-c; reproduced here as Figs 1.12a-c) so-called *Trochammina ochracea* proved to be a planispiral '*Haplophragmoides*'. It is re-illustrated by SEM in Figs 16-18 and it (BMNH no 1955.11.1.5003) clearly shows the same collapse features as the original drawings. In addition to this specimen, we have illustrated for comparative purposes (Figs 19-21), another, somewhat less deformed specimen, from Acupe, Brazil (BMNH no. ZF 5002).

The coiling of Millett's species is planispiral, virtually involute, with 7 or 8 chambers in the final whorl. The aperture is a single interiomarginal equatorial slit with a broad everted border. The intercameral sutures are incurved, occasionally sinuous. We are placing it into the widespread brackish form, 'H'. wilberti Andersen. Millett must have regarded it as a *Trochammina* because of the incurved test seen in edge view.

Cann & de Deckker (1981, pl. 2, figs 1–19) illustrated from ephemeral lakes adjacent to the Coorong Lagoon, South Australia, a series of haplophragmoid forms, in part deformed, which they called *Trochammina* sp. They are very similar to *T. ochracea sensu* Millett and we have also placed them in 'H'. wilberti.

Collapse features occur often in brackish foraminifera. The overall consistency of the agglutinated phase, in particular its thickness and cementation, seems to play a role. In the deformed Millett material it appears that the agglutinated phase is rather weakly developed. In non-deformed specimens of 'H'. wilberti, at our disposal, from brackish localities in Nigeria and New Guinea, the wall structure was analysed using high-resolution scanning electron microscopy of fractured tests. It was found that the wall of these specimens is made up of the organic phase (represented by thin inner and outer sheets and material ('glue') between agglutinated elements), and the agglutinated phase. There were no perforations nor alveolar pseudopores present. This is the characteristic Trochamminina-type wall. In these latter, nondeformed specimens, the agglutinated phase appears to be stronger, perhaps better cemented, than the Millett material from the Malay Archipelago.

DIMENSIONS OF FIGURED SPECIMENS (MALAY SPECIMEN,

BMNH no. 1955.11.1.5003). Maximum diameter — 490 μ m; axial height (thickness) — 125 μ m.

(BRAZILIAN SPECIMEN, BMNH no. ZF 5002). Maximum diameter — 340 µm.

ENVIRONMENT. According to Millett (1899; 363) this species . . . 'has been observed only at Station 3'. It is a good brackish water indicator and occurs in association with *Trematophragmoides bruneiensis* at this locality.

Genus PARATROCHAMMINA Brönnimann, 1979

TYPE SPECIES. Paratrochaminina madeirae Brönnimann, 1979

Paratrochammina simplissima (Cushman & McCulloch, 1948) Figs 1.9, 25–27

- 1899 Haplophragmium nanum Brady; Millett: 360; pl. 5, figs 9a-c (non Brady, 1881).
- 1939 Trochammina pacifica Cushman var. simplex Cushman & McCulloch: 104; pl. 11, fig. 4 (non Friedburg, 1902).
- 1948 Trochanmina pacifica Cushman var. simplissima Cushman & McCulloch: 76 (nomen novum).
- 1956 Trochammina simplissima Cushman & McCulloch; Bandy: 198; pl. 29, figs 14a-c.
- 1979 Paratrochammina simplissima (Cushman & McCulloch); Brönnimann: 10; figs 2,3,6A–J,8A–H (q.v. for full synonymy).

REMARKS. Millett's illustrated specimen, attributed to H. nanum Brady (op. cit. pl. 5, figs 9a-c; reproduced here as Figs 1.9a-c), is a sinistrally coiled specimen with 5 chambers in the final whorl. From the drawings it can be seen that the chambers of the final whorl are strongly compressed in an axial direction and the ultimate chamber is radially elongate. The intercameral sutures are well defined and the agglutinant of the spiral side appears to be distinctly coarser than that of the umbilical side. The aperture, which is an essential generic criterion, is only visible in edge view and its umbilical extension, if any, cannot be seen in the drawing of the umbilical side. We have searched the Millett Collection to find this figured specimen but the closest to it is a dextrally coiled individual (Figs 25-27), so it is possible that Millett's drawings could be reversed. Our figured specimen is undoubtedly Paratrochammina simplissima (Cushman & McCulloch). The single umbilical aperture is an elongate interiomarginal slit in the final septum, which extends from the surface of the first chamber of the final whorl onto that of the penultimate chamber. Its length is about 120 µm and it is lined by a weakly uplifted border of agglutinated fragments. The final whorl has 5 chambers, as in the original drawing, but the ultimate chamber, perhaps, is radially not as elongate as in Millett's figure. The test consists of 10 chambers, the coiling is rather tight and the axial depression (umbilicus) is therefore virtually closed. The radial sutures are well defined on both sides and the outline of the test is weakly lobate; the periphery, as seen in edge view, being compressed but still rounded. The spiral side is almost flat and the umbilical side slightly concave. As in Millett's illustrated specimen, ours is also more coarsely agglutinated on the spiral side than umbilically.

The marine, shallow water P. simplissima differs in all

pertinent features (size, chamber inflation and shape, aperture, etc.) from Brady's deep water species *Haplophragmium* (=*Trochammina*) nanum which was lectotypified, redescribed and illustrated by Brönnimann & Whittaker (1980: 177, figs 1–9). P. simplissima is highly variable in the overall shape and outline of the test (see Brönnimann, 1979: 14, figs 6A–J), however it is usually less compressed axially than Millett's specimens.

DIMENSIONS OF FIGURED SPECIMEN (BMNH no. 1955.11.1.1141). Maximum diameter — 370 µm; minimum diameter — 280 µm; axial height (thickness) — 90 µm.

ENVIRONMENT. According to Millett (1899: 360), this species . . . 'is most abundant in Area 1'. It is a marginal marine species and significantly, was not listed where true brackish species such as *Acupeina triperforata*, *Ammoastuta salsa*, *Arenoparrella mexicana*, etc. were recorded.

Genus *TREMATOPHRAGMOIDES* Brönnimann & Keij, 1986

TYPE SPECIES. *Trematophragmoides bruneiensis* Brönnimann & Keij, 1986.

REMARKS. The genera Haplophragmoides, Cribrostomoides, and Discammina are all superficially similar to Trematophragmoides. Trematophragmoides Brönnimann & Keij is slightly evolute and planispiral with 3 apertures per chamber: a single primary equatorial interiomarginal aperture and one on each side of the chamber, umbilically situated on the suture and posteriorly directed. Haplophragmoides Cushman (1910) is also planispiral but has only one aperture per chamber. Cribrostomoides Cushman (1910) is usually involute, with streptospiral coiling initially, becoming planispiral in the adult whorls; the aperture is a equatorial, single areal slit (with lip) near the base of the septal face, becoming subdivided into a linear series of openings in gerontic forms. Discammina Lacroix (1932) is planispiral and slightly evolute, has a low interiomarginal equatorial aperture and is said to have an . . . 'interior divided by thin straight organic partitions, not corresponding to the original apertural face and not always reflected at the surface' (Loeblich & Tappan, 1987: 68).

Trematophragmoides bruneiensis Brönnimann & Keij, 1986 Figs 1.8, 28–30

- 1899 Haplophragmium compressum Goës; Millett: 359; pl.
 5, figs 8a-c (non Lituolina irregularis var. compressa Goës, 1882).
- 1986 Trematophragmoides bruneiensis Brönnimann &

Keij: 16; pl. 1, fig. 1–10, pl. 2, figs 3–5, pl. 10, figs 1–3, text-fig. 1.

REMARKS. Brönnimann & Keij (1986) described from brackish waters of Brunei, NW Borneo, a planispiral agglutinated foraminifer with an interiomarginal and equatorial primary aperture and two secondary lateral apertures per chamber. The test shape is quite variable and the periphery, as seen in edge view, can be broadly rounded or compressed, almost subcarinate. Millett's roughly agglutinated species (1899, pl. 5, figs 8a-c; reproduced here as Fig. 1.8a-c), attributed by him to Goës' species H. compressum, shows two lateral openings and a single equatorial primary opening per chamber, and is undoubtedly a Trematophragmoides. Our SEM illustrations (Figs 28-30) show the same specimen as that drawn by Millett. As the early radial sutures are indistinct, the total number of chambers cannot be determined with certainty; the final whorl, however, contains 6 chambers. The lateral secondary apertures are well exhibited in Fig. 30 and the equatorial primary aperture in Fig. 29. Although the number of chambers in the final whorl is less than in the types of T. bruneiensis, other features agree well and there is no doubt that the two are one and the same.

DIMENSIONS OF FIGURED SPECIMEN (BMNH no. 1955.11.1.1136). Maximum diameter — 470 μ m; maximum thickness (final chamber) — 200 μ m.

ENVIRONMENT. This species occurs only at Station 3. Millett (1899) does not offer any information about its association with other species, but from a study of his collection it can be seen to occur with *'Haplophragmoides' wilberti*. From this information, Station 3 must have been a brackish locality.

Genus TROCHAMMINA Parker & Jones, 1859

TYPE SPECIES. Nautilus inflatus Montagu, 1808.

Trochammina? milletti sp.nov. Figs 1.10,22–24

1899 Haplophragmium anceps Brady; Millett: 361, pl. 5, figs 10a,b (non Brady, 1884).

DIAGNOSIS. Small conical, tightly-coiled *Trochammina?* with three large subglobular chambers in the final whorl.

NAME. In honour of Fortescue William Millett.

HOLOTYPE. BMNH no. 1955.11.1.1088. Illustrated in Figs 22,23. This may be the specimen figured by Millett (1899, pl. 5, figs 10a,b; reproduced here as Figs 1.10a,b). From Station 12, Area 1.

DESCRIPTION (HOLOTYPES). Test free, dextrally coiled conical trochospire with pointed initial portion. Final volution

Figs 45–47 Ammotium directum (Cushman & Brönnimann). Figs 45,46, Detail of aperture (×975 and ×280, respectively). BMNH no. 1955.11.1.1119; Fig. 47, Side view (×160). BMNH no. ZF 4999, mangrove sediments, Brönnimann sample 93, Acupe, Brazil

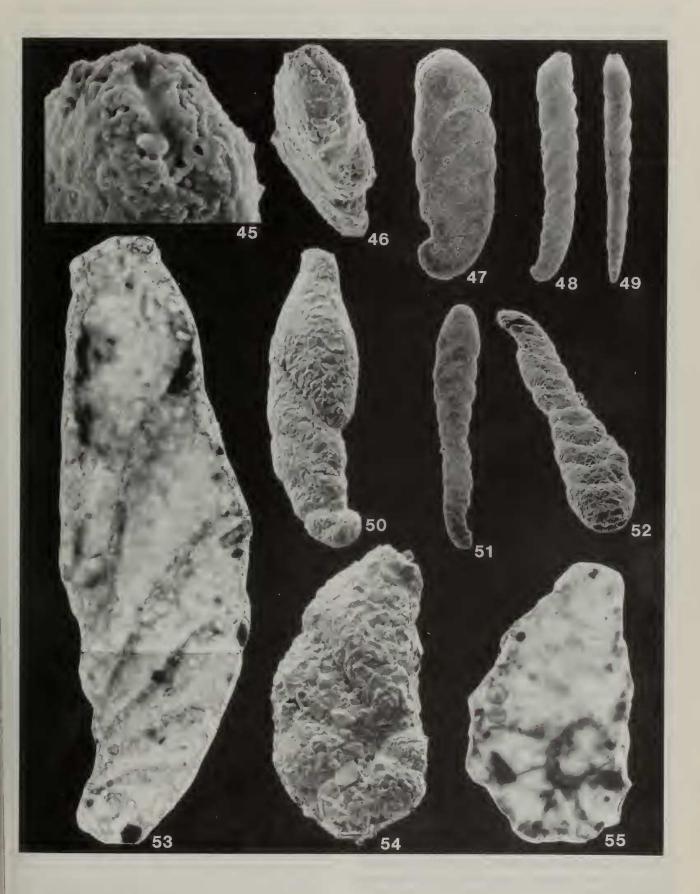
Figs 48, 49, 51, 52 Ammotium subdirectum Warren. Figs 48,49, Side and edge views (×85). BMNH no. ZF 5000; Figs 51,52, Side and oblique-apertural views (×85 and 125, respectively). BMNH no. ZF 5001. Both from mangrove sediments, Brönnimann sample 93, Acupe, Brazil.

Figs 50, 53 Ammotium pseudocassis (Cushman & Brönnimann). Side view (×160) and separate specimen in clearing oil (×265). Brönnimann Collection, mangrove sediments, Guaratiba, Brazil.

Fig. 54 Ammotium morenoi (Acosta). Side view (×205). Brönnimann Collection, mangrove sediments, Guaratiba, Brazil.

Fig. 55 Ammotium distinctum (Cushman & Brönnimann). Side view in clearing oil (×330). Brönnimann Collection, sample 145, from Acupe, Brazil.

All from Millett Collection, Malay Archipelago, except where stated.



triserial, consisting of large subglobular chambers, somewhat compressed in axial direction, making up major part of the test. Coiling tight and axial depression (umbilicus) closed. Sutures well defined. Single interiomarginal aperture a small arch resting with its slightly upturned border completely on surface of first chamber of final whorl. Agglutinant rather coarse.

DIMENSIONS (HOLOTYPE). Height of test — $160 \ \mu\text{m}$; width (umbilical diameter) — $150 \ \mu\text{m}$.

REMARKS. Millett (op.cit., pl. 5,, figs 10a,b) attributed this small, rather fragile, conical form, to Haplophragmoides anceps Brady. The aperture is a broadly rounded interiomarginal arch, sitting with its border completely on the final whorl and therefore the species should belong to Trochammina (see Brönnimann et al., 1983). Fig. 23 illustrates a typical specimen from the Millett Collection but there are extremes (Paratype BMNH no. 1955.11.1.1088; Fig. 24) where the height of the trochospire and the umbilical diameter are about the same or the former even appears to be slightly larger. In 1983, Brönnimann et al. held great store by the fact that in the Trochamminacea the umbilical diameter was invariably greater than the length of the axis of coiling (height of the trochospire), whereas in the Ataxophragmiacea the reverse was true. This is the first time we have found a species, and apparently a single population, at the borderline of the two groups. For this reason we have only tentatively placed this interesting species in Trochammina.

The true *H. anceps* Brady, 1884 is the type species of *Globotextularia* Eimer & Fickert, 1899. This is a robust, deep water form, much larger than Millett's species, with a very high, often irregular coil, an open umbilicus and larger aperture.

ENVIRONMENT. According to Millett (1899: 361), . . . 'specimens [of "H. anceps'] are numerous and well distributed'. They are found at stations 5,11,12 (Area 1) and 27,28 (Area 2). It is associated with the agglutinating foraminifera Ammobaculites exiguus at stations 12 and 27 and rare Acupeina triperforata/Arenoparrella mexicana at Station 5. The former is found in both marginal marine and brackish localities, whereas the latter are true brackish forms. It is therefore not known for certain whether T.? milletti is a marine or a brackish species.

Genus TRUNCULOCAVUS gen.nov.

TYPE SPECIES. Trunculocavus durrandi sp.nov.

DIAGNOSIS. Test free, initially biserial, then abruptly uniserial. Biserial chambers subglobular, uniserial chambers with circular transverse section. Wall agglutinated, of Trochamminina-type. Aperture single, terminal, circular and large, devoid of everted border.

NAME. Derived from the Latin: *cavus*, a hole or hollow, and *trunculus*, tip or end.

REMARKS. Our new genus has the basic morphology of *Bigenerina* d'Orbigny, 1826 (type species *B. nodosaria* d'Orbigny, 1826), but differs in the large circular aperture of the final chamber of the uniserial stage, devoid of a border structure. In contrast, the terminal aperture of *B. nodosaria* is a small central porus with everted border. According to Loeblich & Tappan (1987: 172), *Bigenerina* also has a perfo-

rate ('canaliculate') wall, whereas *Trunculocavus* has a Trochamminina-type wall.

In the Millett material, there are well-preserved specimens of *Trunculocavus durrandi* showing an organic structure within the large rounded aperture. This structure is different from the inner organic sheet (inner organic lining in the sense of Bender, 1989: 278), which occurs along the inside of the wall of the Trochamminina, because it is independent of the agglutinated-organic wall proper. It is suggested that it represents the epidermal layer of the protoplasmic body of the foraminifer. Therefore, we must distinguish between this type of organic structure, as part of the protoplast, and the inner organic sheet which covers the inside of the agglutinated wall of the Trochamminina-type test (see Brönnimann & Whittaker, 1988), which, although has also been produced by the protoplast, is not directly part of it.

This organic structure, or the epidermal layer of the protoplasmic body, occurs inside the terminal aperture of the test, either as a large rounded opening limited by a thickened border (Fig. 7), or it closes the aperture of the test completely and reveals 6 small perforations with tube-like extensions (Fig. 1) along the apertural periphery. This organic structure does not have a counterpart in the agglutinated-organic phase of the wall, another reason for separating it nomenclatorally from the inner organic sheet. In fossil specimens, the epidermal layer of the protoplast will naturally be absent, so it could not be considered taxonomically. At present, therefore, it has no standing in the systematic treatment of these agglutinated foraminifera, which is based on test features alone. It should, however, be remembered that this situation would have to be modified once it becomes possible to take into consideration the features of the living organism.

In a paper by Petrucci et al. (1983: 72-75), there is a taxonomic appendix by Medioli, Scott & Petrucci. In this appendix a new species, Polysaccammina hyperhalina, is introduced which is of interest here because it shows organic features similar to those described for T. durrandi. P. hyperhalina has a large circular terminal aperture with an irregularly finished border, devoid of particular border structures. Medioli et al. (1983: 72, pl. 21, figs 2,3,6,8) described the aperture as invaginated . . . 'to form an inner, backward pointing funnel'. Their pl. 1, figs 1a,2a show the large, rounded aperture is closed on the inside, as in T. durrandi, by an organic structure having in its centre a small circular porus with everted border. Also, as in T. durrandi, this small opening appears to be a different from the aperture of the test and that it represents the epidermal layer of the protoplast, with features which have no counterpart in those of the test wall and which is different from the inner organic lining.

Trunculocavus durrandi sp.nov. Figs 2.1,3-8

1900 Bigenerina digitata d'Orbigny var. Millett: 6, pl. 1, figs 1a,b (non Bigenerina (Gemmulina) digitata d'Orbigny, 1826).

DIAGNOSIS. As for genus; *Trunculocavus* is presently mono-typic.

NAME. In honour if A. Durrand FRMS, the collector of the Malay Archipelago foraminifera described by Millett.

HOLOTYPE. BMNH no. 1955.11.1.187. Illustrated in Figs 3,4. From Station 9, Area 1.

DESCRIPTION (HOLOTYPE. Test free, small and elongate; ini-

tially a subglobular protoconch, followed by 4 pairs of subglobular, biserial chambers, then abruptly uniserial with 3 cylindrical chambers. Aperture large, terminal and central without everted border; the inner organic sheet closing the aperture, however, develops around its circumference, 6 minute pores with tubular borders. Agglutinated wall of granular, but overall smooth appearance. Tubular organic pores have no counterpart in agglutinated phase.

DIMENSIONS (HOLOTYPE). Height of test — 270 μ m; maximum width of test — 75 μ m; diameter of aperture — 35 μ m; diameters of tubular pores around circumference of aperture — 4–5 μ m.

PARATYPES. Two paratypes (BMNH nos. 1955.11.1.188,189) are illustrated in Figs 5–8. In side view, they are as the holotype with a short biserial stage followed by the uniserial stage composed of 2 or 3 cylindrical chambers. Paratype (BMNH no. 1955.11.1.188; Figs 6–8) shows an aperture where the inner organic sheet does not close the opening. The sheet itself has an opening, bordered by a thickened rim, which is virtually of the same diameter as the rounded terminal aperture of the agglutinated phase; there are no minute pores as in the holotype.

DIMENSIONS (PARATYPES). (BMNH no. 1955.11.1.188) Height of test — 230 μ m; maximum width — 90 μ m; diameter of aperture — 40 μ m.

(BMNH no. 1955.11.1.189) Height of test — 240 μ m; maximum width 75 μ m.

REMARKS. Millett's actual figured specimen (1900, pl.1, figs 1a,b; reproduced here as Figs 2.1a,b) could not be recognised with certainty. Millett's drawing, however, shows a specimen with a rather indistinct biserial initial portion of 4 or 5 pairs of chambers, then a 4 or 5-chambered uniserial stage; the uniserial chambers are cylindrical and the large terminal rounded aperture is devoid of an everted border.

ENVIRONMENT. According to Millett (1900: 6), this species is . . . 'confined to Station 9, and the examples, although minute, are moderately abundant'. From the same locality Millett (1899: 358,359) also found Acupeina triperforata, Arenoparrella mexicana, 'Ammobaculites' exiguus, Ammoastuta salsa and Ammotium spp., all brackish, mangrove sediment-dwelling species. It is therefore assumed that T. durrandi also lives in a brackish habitat.

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